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# NOVEL PLANT COMMUNITIES LIMIT THE EFFECTS OF A MANAGED FLOOD TO RESTORE RIPARIAN FORESTS ALONG A LARGE REGULATED RIVER

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## ABSTRACT

Dam releases used to create downstream flows that mimic historic floods in timing, peak magnitude and recession rate are touted as key tools for restoring riparian vegetation on large regulated rivers. We analysed a flood on the 5th-order Green River below Flaming Gorge Dam, Colorado, in a broad alluvial valley where Fremont cottonwood riparian forests have senesced and little recruitment has occurred since dam completion in 1962. The stable post dam flow regime triggered the development of novel riparian communities with dense herbaceous plant cover. We monitored cottonwood recruitment on landforms inundated by a managed flood equal in magnitude and timing to the average pre-dam flood. To understand the potential for using managed floods as a riparian restoration tool, we implemented a controlled and replicated experiment to test the effects of artificially modified ground layer vegetation on cottonwood seedling establishment. Treatments to remove herbaceous vegetation and create bare ground included herbicide application (H), ploughing (P), and herbicide plus ploughing (H + P). Treatment improved seedling establishment. Initial seedling densities on treated areas were as much as 1200% higher than on neighbouring control (C) areas, but varied over three orders of magnitude among the five locations where manipulations were replicated. Only two replicates showed the expected seedling density rank of $(H + P) > P > H > C$. Few seedlings established in control plots and none survived 1 year. Seedling density was strongly affected by seed rain density. Herbivory affected growth and survivorship of recruits, and few survived nine growing seasons. Our results suggest that the novel plant communities are ecologically and geomorphically resistant to change. Managed flooding alone, using flows equal to the pre-dam mean annual peak flood, is an ineffective riparian restoration tool where such ecosystem states are present and floods cannot create new habitat for seedling establishment. This problem significantly limits long-term river and riparian management options. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: cottonwood; demography; environmental flows; fluvial landforms; managed flood; *Populus*; regulated river; riparian vegetation

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## INTRODUCTION

Many of the world's large rivers have been altered by dams and diversions to provide water for irrigation and urban use, hydroelectric power and recreation as well as flood protection (Petts, 1984; Dynesius and Nilsson, 1994; McCully, 1996; Postel and Carpenter, 1997). These structures and the hydrologic changes produced by their operation have fragmented river systems (Graf, 1985) and produced undesirable impacts to downstream ecosystems, including changes in fluvial landforms (Collier *et al*., 1996; Webb, 1996; Merritt and Cooper, 2000), fish and aquatic invertebrate communities (Vinson, 2001; Fausch *et al*., 2002) and the collapse of riparian forests (Rood and Heinze-Milne, 1989). Recognition of the critical ecological services lost due to hydrologic alterations has stimulated a number of ecological restoration efforts, and more recently, the proposal of river restoration standards (Jansson *et al*., 2005a; Palmer and Bernhardt, 2005).

Flow requirements to sustain riparian ecosystems have been calculated for rivers in many parts of the world, including Australia (Arthington *et al*., 2006), Europe (Hughes *et al*., 2005), South Africa (Acreman *et al*., 2000), Canada (Rood and Mahoney, 1990, 2000) and the US (Stromberg and Patten, 1990; Richter and Richter, 2000; Merritt *et al*., 2010; Poff *et al*., 2010; Richter, in press). An important restoration tool is the use of managed flow releases from dams to meet a wide range of ecological, geomorphic and human needs (Patten and Stevens, 2001). These include the reduction of soil salinity, improvement of floodplain plant growth, providing water for flood recession farming (Senegal River in West Africa; Acreman *et al*., 2000), initiating geomorphic change (Colorado River, Grand Canyon, Arizona; Schmidt *et al*., 2001), and facilitating riparian plant establishment (Truckee River, Nevada: Rood *et al*., 2003; Rood *et al*., 2005, Bill Williams River, Arizona: Shafroth *et al*., 2010).

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Dam releases for environmental purposes often involve discharges larger than those required for other management activities. Nevertheless, most managed high flows have been of small magnitude and short duration relative to historic (natural) floods. For example, the widely publicized 1996 Colorado River experimental flood release from Glen Canyon Dam peaked at only ~35% of the pre-dam mean annual peak discharge (mean $Q_{\mathrm{MAX}}$), and its beneficial effects on sand bar formation (Schmidt *et al*., 2001), riparian vegetation (Kearsley and Ayers, 1999) and juvenile native fishes (Hoffnagle *et al*., 1999) were relatively short-lived. Standards for large managed flood flows are almost non-existent (Acreman, 2003), despite such flows being critical for rejuvenating riparian habitat along many rivers (Scott *et al*., 1996; Friedman and Lee, 2002; Cooper *et al*., 2003).

The geomorphological and ecological effects of a managed flood are influenced by both flow and local riverine ecosystem characteristics. For example, a flood will produce different increases in river stage, erosion or sediment deposition on low- versus high-gradient stream reaches, and in constrained versus unconstrained valleys. In addition, river segments subjected to decades of regulated flows may support fluvial landforms and vegetation types strikingly different from those present prior to dam construction (Johnson, 1994; Stevens *et al*., 1995; Merritt and Cooper, 2000; Johnson, 2002). These novel post-dam riverine ecosystems may represent an ecological state that resists change back to the pre-dam state even if hydrologic conditions similar to the pre-dam environment are periodically reintroduced to the system (Suding *et al*., 2004; Wolf *et al*., 2007). Whether such novel and resistant states are common below dams is unclear, because few studies have examined the effect of large (relative to pre-dam flows) dam releases on downstream ecosystems.

Managed floods result in readily quantifiable losses of electric power generation revenues and water for downstream users. They may also incur a cost by damaging downstream infrastructures and disrupting reservoir related recreation. It is critical for both the public and water and land management agencies to have realistic expectations of the potential benefits of any managed flood, and particularly for unusually large flows (Hughes and Rood, 2003). Thus, experiments in a wide range of regulated river systems are needed to clarify what can and cannot be accomplished with managed floods of different magnitude.

Throughout the western US and Canada, large river riparian ecosystems were historically dominated by species of cottonwood (*Populus* spp.). Most of these rivers are now regulated, and many riparian forests along those that are regulated produce few recruits (Rood and Mahoney, 1990; Scott *et al*., 1996; Cooper *et al*., 2003). In addition, large numbers of trees have died, and survivors have experienced branch and root system dieback (Rood *et al*., 2000; Williams and Cooper, 2005), both of which reduce seed production and may constrain future restoration opportunities (Reily and Johnson, 1982; Rood and Heinze-Milne, 1989; Rood *et al*., 1995; Rood *et al*., 2000; Williams and Cooper, 2005). The Colorado River and its major tributaries represent one of the world's most regulated river systems (Graf, 1985) and its cottonwood-dominated riparian ecosystems have been severely degraded in many areas (Patten, 1998; Andersen *et al*., 2007). We implemented a landscape-scale experiment in conjunction with a large managed flood on a major tributary, the Green River, to determine whether an unusually large managed flood can be used to establish new tree cohorts in riparian zones. We addressed two questions: (1) will a controlled flood lead to recruitment of an ecologically significant quantity of native trees if the flood's hydrologic character (duration, peak magnitude, timing and rate of recession) matches conditions known to have effectively led to tree recruitment on the same river segment prior to regulation?, and (2) if not, what additional measures are necessary to restore cottonwood recruitment processes?

Our results serve as a case study providing insight into the benefits and limitations associated with the use of managed floods as a restoration tool. We demonstrate that altered flow regimes can lead to landscape states that are highly resistant to flood perturbation. Our results have important implications both for restoring riparian vegetation below older dams where such regulated flow regimes have long been in place, and for minimizing undesirable vegetation change downstream from recently completed or planned dams.

## STUDY REACH

We worked on a 16-km long, 5th-order reach of the Green River in Browns Park National Wildlife Refuge, Colorado (Figure 1). Browns Park is a large alluvial valley (elevation 1635 m) with hot summers and cold winters. The climate is semi-arid, with a mean annual precipitation of 21 cm (based on years 1966–1997; US National Weather Service for Browns Park Refuge, Colorado; http://www.hprcc.unl.edu/wrcc/states/co.html, accessed 13 July 2006). The study reach has low gradient, meanders and a sand-bedded channel.

### *History of Green River flows and Flaming Gorge Dam operations*

The pre-dam Green River in Browns Park had a mean $Q_{\mathrm{MAX}} = 317\ \mathrm{m^3\,s^{-1}}$ (1929–1962 data; standard deviation = $119\ \mathrm{m^3\,s^{-1}}$; Figure 2 top panel). Flaming Gorge dam and power plant construction was completed and reservoir filling began in the fall of 1962. The reservoir filled for the first time in 1967. The dam has three outlets for water: (1) power



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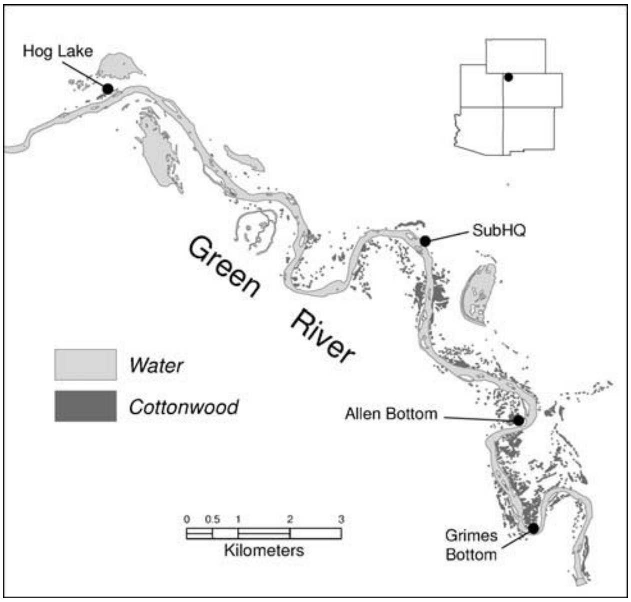


Figure 1. Map of the Green River in lower Browns Park, in northwest Colorado (inset) showing the four locations where treatments were applied (Hog Lake, SubHQ, and Allen and Grimes bottoms). The river flows from left to right. The map also shows the location of individual trees and stands of mature Fremont cottonwood on the Green River floodplain. Note the small amount of cottonwood in the upstream portion of the mapped area, including the Hog Lake study site. The cottonwood map is from Crawford (1997).

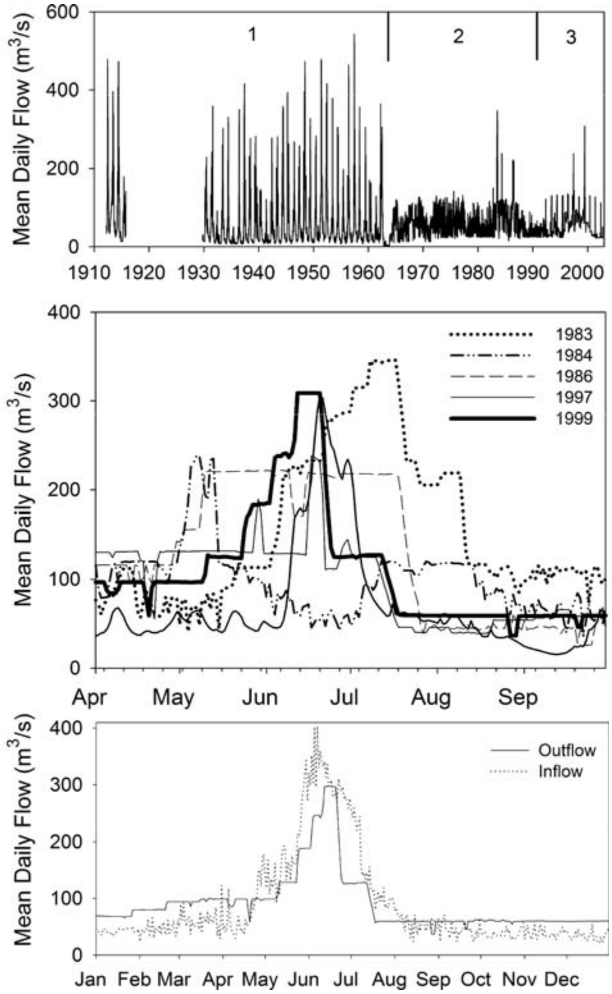


Figure 2. *Top panel*: mean daily flow of the Green River. Period 1 is the pre-Flaming Gorge Dam period, 2 is the post dam period prior to dam management for endangered fishes and 3 is the post dam period managed for endangered fishes. *Middle Panel*: mean daily flow of the Green River for 1983, 1984, 1986, 1997 and 1999. *Bottom Panel*: mean daily inflow to and outflow from Flaming Gorge Reservoir.

generating turbines that can pass $130\,m^3\,s^{-1}$, (2) two bypass tubes that can each pass $113\,m^3\,s^{-1}$ and (3) a spillway that can pass $793\,m^3\,s^{-1}$. From 1963 to 1984 Flaming Gorge Dam was operated with few flow management constraints other than maintaining a minimum downstream flow of $23\,m^3\,s^{-1}$ to promote a tailwater trout fishery (Muth *et al.*, 1993). Management objectives included maximizing power generation, maintaining a full reservoir pool and avoiding use of the bypass tubes and spillway. As a result, large daily flow variations occurred and the seasonal timing of high and low flow events was independent of natural hydrologic processes. Historically, $Q_{MAX}$ occurred in May or June, during the snowmelt runoff period in the headwater areas in the central Rocky Mountains. However, from 1963 to 1982 this pattern occurred in only two years, and $Q_{MAX}$ often occurred in winter. From 1985 to 1992 flows were managed to reduce negative impacts on native fish species, with relatively low flows in August and September, and daily fluctuations limited to a maximum of $68\,m^3\,s^{-1}$. While these flows mimicked the timing of the annual low flow, they have been of much greater magnitude than historic low flows. In 1993, management scenarios developed to protect and enhance populations of federally endangered native fish species were implemented, with releases at peak power plant capacity in spring and lower flows of $31–51\,m^3\,s^{-1}$ in summer and autumn (US Department of the Interior, 2004). The current operating plan recommends early summer peak flows, with magnitude and duration based upon reservoir inflows. Peak flows would be larger and/or longer in high snowpack years. However, flows equal to or larger than those of 1997 or 1999 are unlikely as they require the use of the spillway (US Department of the Interior, 2004).

Very high snowmelt runoff inflows to Flaming Gorge reservoir necessitated dam outflows that greatly exceeded power plant capacity in 1983, 1984, 1986, 1997 and 1999 (Figure 2 middle panel). The 1983 inflows filled the reservoir and necessitated emergency releases that utilized the power plant, jet tubes and spillway, and produced the highest post-dam flow to date ($388\,m^3\,s^{-1}$; middle panel). The 1984 managed flood was of short duration but occurred in early summer, while the 1986 peak release was sustained



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at 227 $m^3 s^{-1}$ from early May through late July. The 1999 flood, the effects of which are analysed in this paper, mimicked the natural (unregulated) inflows to Flaming Gorge Dam in seasonal timing and the rate of flow increase and decrease (Figure 2 bottom panel). However, the reservoir inflow in 1999 peaked at 404 $m^3 s^{-1}$ whereas the maximum outflow peaked at 317 $m^3 s^{-1}$, a value identical to the mean pre-dam $Q_{MAX}$.

### *Regulation-induced changes to fluvial landforms and riparian vegetation*

The Green River channel's initial response to flow regulation in the study reach was to narrow by ~30 m (Merritt and Cooper, 2000). Unvegetated point bars were colonized by woody plants, particularly *Tamarix* spp. and herbaceous dicots (Merritt and Cooper, 2000; Grams and Schmidt, 2005). However, after the 1980's the channel widened and developed parallel vertical banks nearly 3 m tall at low flow, and islands supporting dense marsh vegetation formed in the channel. By 1999, the floodplain at elevations immediately above those corresponding to river stage at power plant capacity was covered by dense stands of sandbar willow (*Salix exigua*) or other woody and herbaceous riparian plants, due to a perennially high water table and the lack of inundation, scouring, or sediment deposition (Merritt and Cooper, 2000). Over the same period, the riparian forest, composed solely of Fremont cottonwood [a common name regionally attached to the ecologically similar *Populus fremontii* subsp. *fremontii* S. Watson and *P. deltoides* subsp. w*islizenii* (S. Watson) Eckenwalder, as well as their intergrades; taxonomy follows Eckenwalder (1977)] deteriorated through death of individual trees, loss of branches on surviving trees, and an almost complete lack of recruitment (Cooper *et al*., 2003; Williams and Cooper, 2005), which in this species is almost entirely sexual. Desert shrubs now dominate much of the higher floodplain surface. These novel landforms and vegetation types are distinctly different from the bare point bars, and cottonwood-dominated floodplains that occurred prior to river regulation, when floods of average to high magnitude led to successful cottonwood establishment.

### *Study locations*

We worked at three locations that represented fluvial landforms common along the Green River: a point bar (Grimes Bottom) and two disjunct abandoned channels (Sub-Headquarters and Hog Lake; Figure 1). The particular locations chosen were the only places within the study reach both of sufficient size to support our field experiment and that we expected to be inundated by the 1999 experimental flood, which had a planned peak discharge of ~340 $m^3 s^{-1}$. Our expectation of inundation was based upon observations of maximum river stage reached during an earlier, smaller managed flood (~240 $m^3 s^{-1}$ peak release in 1997). The Grimes Bottom and Hog Lake locations were divided into adjacent upstream (upper) and downstream (lower) sites, whereas the Sub-Headquarters location contained a single site. We also monitored recruitment at a third abandoned channel site we expected to be inundated, Allen Bottom (Figure 1), but we performed no manipulation there because of access difficulties. We consider this fourth location to be a secondary study site.

## METHODS

### *Experimental design*

Our primary goals were to determine (1) whether pre-flood vegetation manipulation (artificial disturbance) was necessary for cottonwood seedling recruitment, and (2) whether the level of recruitment increased with intensity of artificial disturbance. We anticipated there might be variation in tree seedling recruitment due to differences among the locations, so we chose to test for a treatment effect using a randomized complete block experimental design, with locations as blocks. We divided each of the five primary study sites into four 10- by 30-m areas, each with its long axis parallel to the river. We then randomly assigned each of four possible treatments to one of the four areas within each site: herbicide application (H), ploughing (P), herbicide application followed by ploughing (H + P) or control (C). The control area was not manipulated in any way. The H treatment was a single application of an imazapur-based chemical (Roundup®) to the canopy of all plants present 1–2 weeks prior to the onset of flooding. The goal of herbicide application was to chemically kill or stress existing vegetation and remove shade and inter-specific competition that can hinder seedling establishment. The P treatment, performed using a disk pulled behind a tractor, was intended to both reduce interspecific competition and increase the area of bare ground. We assumed the bare ground produced by the P treatment would make it more effective than the H treatment in promoting seedling establishment, and the H + P treatment would increase bare ground and maximally suppress competitors. Thus, we predicted the rank of the treatments, in terms of seedling establishment success, to be P + H > P > H > C.

We randomly located 10 (rarely 11) points within each control and treatment area to serve as the centre of a 1- to 4-m diameter sampling plot. We placed 19 such plots at the secondary Allen Bottom site. We counted individual cottonwood plants (members of the 1999 cohort) present in each plot monthly during the first two growing seasons after the 1999 flood event (all locations), and three times yearly during years 3–5 and once in year 9 (primary



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locations only). Where initial seedling density was low we used the larger plot size (Table I). Within plots, we analysed soil collected from the top 10 cm at the plot centre for per cent carbon and nitrogen on a LECO CHN1000 analyser (LECO, St. Joseph, Michigan, USA), and for particle size distribution (hydrometer method; Gee and Bauder, 1986). Sampling was done only after the controlled flood. We measured volumetric soil water content in each sampling plot at depths of 0–15 and 0–30 cm each month during the summer of Year 1 using a Moisture Point® time domain reflectometry unit with custom 3-mm diameter probes (Environmental Sensors Inc., Victoria, British Columbia, Canada). Soil water content was recorded as the mean of three measurements at each depth. Total herbaceous plant biomass in each treatment area at the end of the first growing season, an index of the relative effectiveness of our manipulation methods, was determined by clipping a 0.5-$m^2$ subplot from within each plot.

We measured sediment deposition resulting from the flood using square Plexiglas disks (400 $cm^2$) anchored to the ground surface with a metal spike driven through a hole drilled in the disk's centre. Following the flood event, we relocated the disks and measured the thickness of overlying sediment. We also established 100 sediment disks on six islands in the Green River to measure flood sediment deposition on islands relative to sediment deposition in our study plots. Twenty disks were installed systematically on four larger islands and 10 disks on two smaller islands.

We measured cottonwood seed rain density weekly at each of the five primary study sites using sets of five 400-$cm^2$ boards coated with Tanglefoot®, and mounted parallel to the ground surface at a 1-m height. Six traps were placed at the Allen Bottom study site. We monitored water table dynamics using monitoring wells ($n = 2$ per location).

### *Data analysis*

We tested for a treatment effect using a randomized complete block ANOVA with unbalanced replication ($n = 2$ at Grimes and Hog, but $n = 1$ at Sub-Headquarters). We used the mean value of the variable of interest (e.g. seedling density) within each experimental unit (= treatment area) in the analysis, and performed a $\log_{10}$ transformation on density data to reduce heteroscedasticity. Based on our expectation that treatment area mean seedling density would increase with disturbance intensity ($C < H < P < H + P$), we designed contrasts for the following treatment pair means: $H + P = P$, $P = H$, and $H = C$. We adjusted $\alpha$ for each of the multiple comparisons using the Bonferroni procedure to $0.05/3 = 0.017$.

We used the same form of ANOVA to test for a treatment effect on seedling survivorship during the 1999 growing

Table I. Treatment and plot arrangements among study locations and sites along the Green River in Browns Park National Wildlife Refuge, northwest Colorado. Standard deviation is included with tabulated values for mean site elevation and soil N and C levels

| Location | Site name | Plot diameter (m) | Treatments | Number plots per treatment[a] | Mean plot elevation[b] (m) | Max depth to ground water (cm)[c] | %N (mass basis) | %C (mass basis) | Cottonwood seed rain (seeds $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|
| Grimes Bottom | Lower Grimes | 2 | C,H,P,P + H | 10 | $1.39 \pm 0.018$ | 156.4 | $0.037 \pm 0.015$ | $1.13 \pm 0.26$ | 372 |
| | Upper Grimes | 2 | C,H,P,P + H | 10 | $1.36 \pm 0.020$ | 149.0 | $0.051 \pm 0.029$ | $1.52 \pm 0.65$ | |
| Sub-Headquarters | Sub-HQ | 4 | C,H,P,P + H | 10 | $0.91 \pm 0.014$ | 116.7 | $0.049 \pm 0.020$ | $1.68 \pm 0.38$ | 55 |
| Hog Lake | Lower Hog | 4 | C,H,P,P + H | 10 | $0.87 \pm 0.010$ | 136.2 | $0.045 \pm 0.017$ | $1.35 \pm 0.28$ | 7.5 |
| | Upper Hog | 4 | C,H,P,P + H | 10 | $1.18 \pm 0.009$ | 95.3 | $0.046 \pm 0.018$ | $1.38 \pm 0.27$ | |
| Allen Bottom | Allen | 1 | C | 19 | $1.17 \pm 0.024$ | 102.5 | $0.051 \pm 0.033$ | $1.50 \pm 0.48$ | 879 |

[a] A few treatments contained 11 plots.
[b] Mean plot elevation ($\pm$ SE) for a site is referenced to local river stage at the time the survey was conducted. Survey dates differed among sites, but the nearly equal daily mean discharge values (range 59.3–59.5 $m^3 s^{-1}$) on the survey dates allow elevations to be meaningfully compared across sites.
[c] Post-flood ground water depth measured in September 1999.



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season. The proportion surviving in each plot was transformed (arcsine square-root) and the mean of the transformed values for each treatment area was used in the analysis. Treatment area mean values presented in the text (as mean $\pm$ SE) are untransformed. We also used the same form of ANOVA to evaluate the effectiveness of our vegetation manipulations, using the mean treatment area plant biomass values. We expected biomass to decrease with disturbance intensity: C > H > P > P + H.

To gain insight into factors potentially contributing to differences in recruitment among locations, we used two-way ANOVA to test for equality in plant biomass (control treatments only) and in initial soil nitrogen and organic carbon among the three locations and five primary sites. Proportions were arcsine-square root transformed prior to analysis. Because we randomly selected sample points within the treated areas and controls, we considered these sample points to be replicates, and followed the test for main effects with Bonferroni-adjusted pairwise comparisons where appropriate. We expected to find differences among but not within locations. All statistical analyses were preformed using SYSTAT® 11.

The flood event as well as the study reach is unreplicated, so our conclusions are derived solely from this one managed flood in Browns Park. However, our conclusions regarding the relative benefit of the various disturbance treatments are statistically valid for application to our study area and can be cautiously applied to other regulated river reaches.

## RESULTS

### *Seed rain, soil chemistry and effectiveness of disturbance*

Seed rain during the summer of 1999 varied greatly among the study sites, from 7.5 seeds $m^{-2}$ $year^{-1}$ at Hog to 879 seeds $m^{-2}$ $year^{-1}$ at Allen Bottom (Table I). In contrast, our premise that soil chemistry was similar across locations was supported by the two-factor ANOVA examining soil N, which indicated no difference in control area soil N among the three primary locations ($p = 0.90$), but a significant difference among the five primary sites ($p = 0.025$). The single significant pairwise comparison indicated soil N was lower in Lower Grimes than in Lower Hog ($p = 0.002$). The difference in the means was ~18% (Table I).

Productivity, as indexed by plant biomass in control areas near the end of the 1999 growing season, differed among primary locations ($F = 7.59$; df = 2, 45; $p = 0.001$) but not sites ($F = 0.05$; df = 2, 45; $p = 0.98$), with the point bar (Grimes Bottom) producing nearly five times more biomass than the abandoned channel locations (Sub-Headquarters and Hog Lake). The secondary Allen Bottom location, however, supported even higher plant biomass than Grimes (mean $\pm$ SE: $137 \pm 17.8$ g $m^{-2}$ vs. $63 \pm 10.3$ g $m^{-2}$, respectively). The ANOVA (blocking by site) evaluating effectiveness of the manipulations in reducing pre-existing vegetation indicated a treatment effect on mean plant biomass ($F = 5.98$; df = 3, 12; $p = 0.010$). Subsequent, Bonferroni pairwise comparisons indicated that biomass in the control treatment was greater than in any other treatment ($p \leq 0.031$), but no difference among the three types of manipulation was detectable.

### *Seedling establishment*

The ANOVA comparing mean seedling densities in autumn 1999 indicated a treatment effect (Table II). Very few seedlings established at Upper Hog, leading us to drop that site as a replicate. However, analyses including that site both with empty cells and with assigned minimum cell values (1 seedling per treatment area) produced results qualitatively identical to those presented here. The treatment least square means followed our predicted ranking of P + H > P > H > Control. The planned contrasts indicated that the disturbance treatments differed from the control (Table II), but there was no difference among the three disturbance types. Examination of the treatment area mean densities (Figure 5, Top Panel) showed the lack of difference among the disturbance types was the result of variation in their ranks among locations. The two replicates at Grimes, where seedling density was greatest, showed the expected pattern of density increasing with treatment intensity [C → H → P → H + P]. In contrast, the set of treatments at Sub-Headquarters and Hog showed mixed patterns, with lowest seedling density in the control as expected, but

Table II. Results of randomized complete block ANOVA and planned contrasts* comparing autumn seedling densities in treatments following the 1999 Green River experimental flood (Upper Hog site deleted)

| Source | SS | df | MS | *F*-ratio | *p* |
|---|---|---|---|---|---|
| Treatment | 30.89 | 3 | 10.30 | 14.15 | 0.0006 |
| Block | 30.08 | 2 | 15.04 | 20.67 | 0.0003 |
| Error | 7.28 | 10 | 0.73 | | |
| Contrasts: | | | | | |
| [P + H] > [Plough] | 0.201 | 1 | 0.201 | 0.28 | 0.31 |
| [Plough] > [Herb] | 1.77 | 1 | 1.77 | 2.44 | 0.07 |
| [Herb] > [Control] | 10.51 | 1 | 10.51 | 14.44 | 0.0017 |
| Error | 7.28 | 10 | 0.728 | | |
| (same for all contrasts) | | | | | |

*We predicted mean density would vary as P + H > P > H > C. Treatment areas were blocked by location. Each contrast was judged is significant if $p < 0.017$.



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highest density in the H treatment (Figure 5, Top Panel). July seedling density at a location (measured in H + P plots except at Allen Bottom) was positively related to the seed rain received (Figure 4).

*Seedling growth*

Excluding the two Hog sites, where no 1999 cohort seedlings survived, mean cottonwood seedling height at the end of the second growing season (September, 2000) differed among the SubHQ and two Grimes sites (2-factor ANOVA without replication: $F = 13.2$; df = 2, 4; $p = 0.017$), but not among treatments ($F = 2.28$; df = 2, 4; $p = 0.22$). Seedlings in all treatments grew fastest at Upper Grimes (Figure 5, Bottom Panel).

We detected no relationship between the autumn 2000 mean seedling height and the total plant biomass within a plot (linear regression, sites and treatments pooled, $n = 33$, $p = 0.27$). However, mean autumn 2001 seedling height for a plot was positively related to the number of live seedlings in that plot (linear regression, sites and treatments pooled, $p = 0.01$, $r^2 = 0.29$).

*Seedling survivorship*

The ANOVA indicated that survivorship to September 1999 differed among treatments (Table III). The only significant contrast was that between the C and H treatments, mirroring the results for seedling density.

Multiple regression analysis of mean treatment area seedling survivorship through the first growing season against the mean values of potential explanatory factors in that treatment area (per cent sand, per cent clay, soil nitrogen content, soil carbon content, soil C:N ratio, autumn plant biomass and mean post-flood water table depth thru July) detected no significant relationship, although a link to soil C:N ratio was marginally so ($p = 0.052$; $R^2 = 0.20$, $n = 19$).

By autumn 2002 only 15 plots still contained cottonwood seedlings, distributed among Upper Grimes (6 plots), Lower Grimes (3) and Sub-HQ (6) (Figure 3). These plots were distributed among H (4), P (6), and P + H (5) treatments and contained a total of 82 individuals. Twelve plots contained $\leq 4$ saplings and 1 contained $>11$. The latter was a plot in the P + H treatment at Upper Grimes that contained >50% of all tallied seedlings (43 individuals). There were no seedlings alive at the secondary Allen Bottom location.

Re-examination of the primary study site plots in 2008 revealed a single live sapling from the 1999 cohort at SubHQ and 15 saplings at Grimes (Table IV). All surviving individuals were in P or P + H treatments. Mean survivorship in those treatments between 2000 and 2008 was 0.623 year$^{-1}$. Dead saplings were particularly common at Grimes, where evidence of recent ungulate rubbing damage and herbivory by both beaver and ungulates was widespread.

Table III. Results of randomized complete block ANOVA and planned contrasts* comparing seedling survivorship through the 1999 growing season in treatments following the 1999 Green River experimental flood (Upper Hog site deleted)

| Source | SS | df | MS | *F*-ratio | *p* |
|---|---|---|---|---|---|
| Treatment | 1.617 | 3 | 0.539 | 7.35 | 0.007 |
| Block | 0.155 | 2 | 0.077 | 1.06 | 0.38 |
| Error | 0.734 | 10 | 0.734 | | |
| Contrasts: | | | | | |
| [P + H] > [Plough] | 0.019 | 1 | 0.019 | 0.254 | 0.31 |
| [Plough] > [Herb] | 0.081 | 1 | 0.081 | 1.110 | 0.16 |
| [Herb] > [Control] | 0.550 | 1 | 0.550 | 7.49 | 0.010 |
| Error | 0.734 | 10 | 0.073 | | |
| (same for all contrasts) | | | | | |

*We predicted survivorship would vary as P + H > P > H > C. Treatment areas were blocked by location. Each contrast was judged significant if $p < 0.017$.

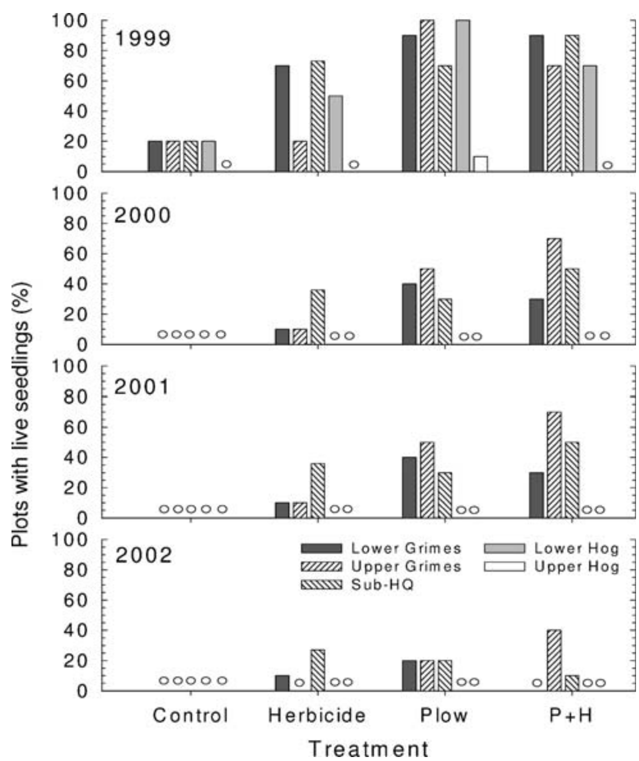


Figure 3. Proportion of plots within each treatment-site combination that contained at least one cottonwood seedling at the end of the indicated growing season. Treatments were imposed in 1999, prior to the experimental flood release, and the sites received no further manipulation. The small open circles indicate cases where no plot in the treatment-site combination contained a live cottonwood seedling.



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Table IV. Survivorship of seedlings established as a result of the 1999 bypass flow over the 9-year period 2000–2008

| Site | Treatment | Number seedlings in 2000 | Number live saplings in 2008 | Survivorship (per year)[a] |
|---|---|---|---|---|
| Hog Upper | C, P, P + H, and H | 0 | — | — |
| Hog Lower | C and P | 0 | — | — |
| | P + H | 5 | 0 | <0.5 |
| | H | 1 | 0 | <0.5 |
| SubHQ | C | 0 | — | |
| | P | 2 | 1 | 0.92 |
| | P + H | 7 | 0 | <0.5 |
| | H | 15 | 0 | <0.5 |
| Grimes Upper | C | 0 | — | — |
| | P | 185 | 4 | 0.62 |
| | P + H | 244 | 10 | 0.67 |
| | H | 10 | 0 | <0.5 |
| Grimes Lower | C | 0 | — | |
| | P | 107 | 1 | 0.56 |
| | P + H | 152 | 0 | <0.5 |
| | H | 10 | 0 | <0.5 |

[a]*Note*: Entries of <0.5 are presented for comparison only; the actual values are unknown. A survivorship of 0.5 year$^{-1}$ results in a probability of fewer than 4 individuals out of 1000 surviving through an 8-year period [*P* (survival over 8 years) = 0.00391].

*Sediment deposition*

The flood deposited sediment on most disks on islands in the river channel (93 of 94 disks that could be relocated, out of 100 installed prior to the flood). Sediment thickness averaged 22.6 ± SE 1.8 cm, but spatial variation was large

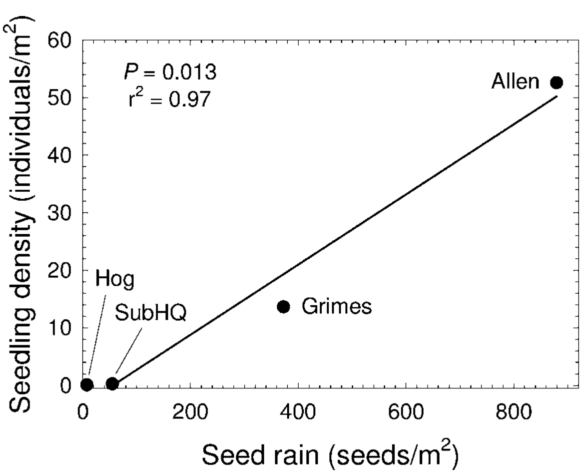


Figure 4. Maximum post-flood seedling densities in the P + H treatments, which were both treated with a herbicide and ploughed, as a function of local seed rain. Plotted data for Hog and Grimes study sites are means for the Upper and Lower sets of plots. The linear regression suggests that about 6% of arriving cottonwood seeds became a recognizable seedling.

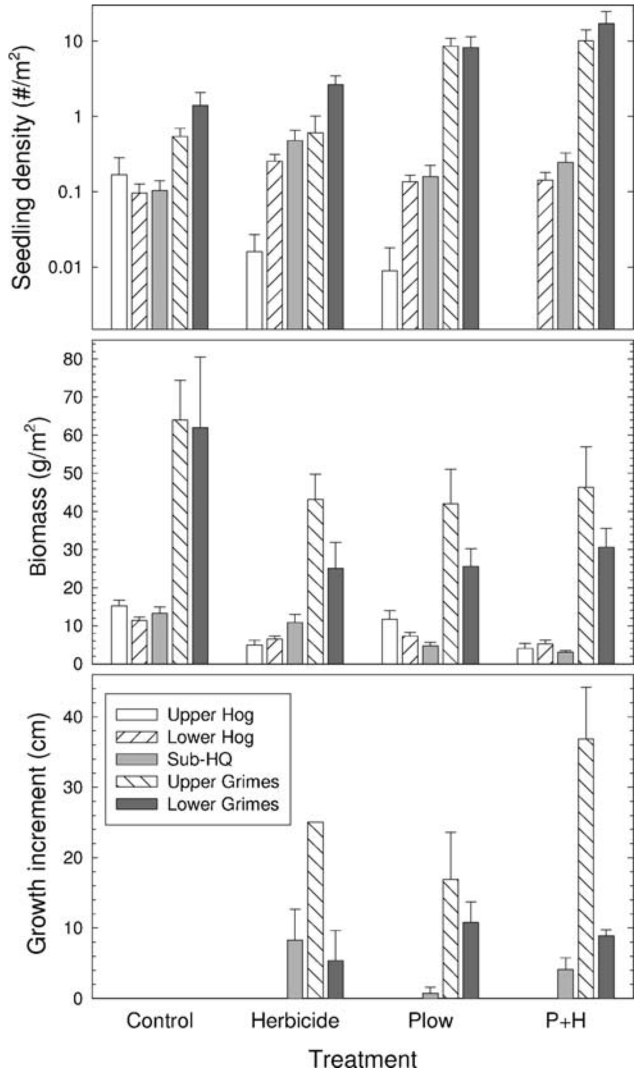


Figure 5. Site by treatment comparisons of post-flood cottonwood germinant density and 2nd-year growth of surviving cottonwood seedlings. Error bars are 1 SE. *Top panel*: Maximum germinant density in the immediate post-flood 1999 growing season. *Middle panel*: total plant biomass present at the end of the 1st growing season (Autumn, 1999), an index of the potential competition cottonwood seedlings faced for soil resources and light. *Bottom panel*: the height growth increment during the 2nd growing season (June–August, 2000). Absence of bars in the bottom panel indicates that no live seedlings were present.

on each island. For example, sediment deposits measured on one island (mean depth 25.9 ± SE 5.4 cm) ranged from 0 to 79 cm deep. Deposition was typically greatest near the upstream end (in thick willow vegetation) or along the island's sides, with the result that sediment deposition enlarged the parabolic shape of the islands. The thickest deposits were in dense sandbar willow stands, where seedling establishment did not occur. Most (59 of 100) treatment plot disks had no sediment deposited on them. Thirteen treatment disks receiving sediment had ≤1 cm and



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only 8 disks had a deposit $\geq$10-cm thick. The mean sediment thickness was $3.5 \pm$ SE 1.2 cm.

## DISCUSSION

This study demonstrates that a managed flood with a peak flow equalling the pre-dam average peak, and appropriate timing and recession rate will not necessarily restore riparian tree recruitment to reaches where it has been eliminated by flow regulation. The persistence of cottonwood forest in our study area depends upon the establishment of new cohorts from seeds transported by wind or water to moist patches of bare fluvial sediment. Germinants must subsequently survive physical and biotic disturbances before reaching sexual maturity (Cooper *et al*., 1999; Andersen and Cooper 2000). On rivers featuring a natural flow regime, patches meeting germination requirements and providing germinants with a relatively high probability of subsequent survival are created through the hydrologic and geomorphic processes driven by floods having a peak magnitude near or above average, a flood recession that coincides with seed rain, and a recession rate that maintains soil moisture conditions conducive to seedling growth (Scott *et al*., 1996; Cooper *et al*., 2003).

Although a flood of appropriate timing, peak magnitude, and rate of recession is necessary for recruitment, our results indicate that the flood alone may be insufficient to trigger recruitment. Both the 1997 and 1999 peak flows (two of the three largest flows since completion of Flaming Gorge Dam in 1962; see Figure 2) were of suitable magnitude, duration, and timing to have triggered Fremont cottonwood establishment in the pre-dam period (Cooper *et al*., 2003), yet we found little or no establishment outside of our manipulated plots. Our data support the hypothesis that 36 years of sediment capture and flow regulation by Flaming Gorge Dam have transformed fluvial landforms and vegetation in the study reach into what may be alternative ecological states resistant to disturbance from managed floods, including vegetated point bars, wetland marshes on islands, and upland deserts in mature cottonwood forests and abandoned channels that offer little or no potential for cottonwood seedling establishment, even if flows formerly appropriate for recruitment are added to the prevailing managed flow regime. The resistance of these novel patch types to cottonwood recruitment by the relatively large 1999 flood pulse is evidence of their stability.

Other examples of new and potentially stable patch types on a regulated river are the wetland marshes on islands within the channel, and desert upland shrubs replacing riparian mesquite (*Prosopis glandulosa* Torrey) and tamarisk (*Tamarix* spp.) forests along the Colorado River in the Grand Canyon (Stevens *et al.*, 1995; Schmidt *et al*., 1998; Stevens *et al*., 2001). These novel patch types are analogous to the vegetated islands and desertified former cottonwood forest in our study area.

Our results suggest that there is a relatively narrow range in the flood pulse component of the natural flow regime within which major ecosystem components and processes are maintained. When dam operations shift the flow regime outside of this normal range of seasonal and interannual variation (Poff *et al*., 1997; Michener and Haeuber, 1998), the processes maintaining the 'normal' state are lost and the formation of new (and potentially flood disturbance resistant) states becomes likely. The threshold initiating the ecosystem shift could be associated with any flow regime-dependent variable causally linked to riparian plant population processes (Bendix and Hupp, 2000; Bornette *et al*., 2008), including depth to ground water (Lite and Stromberg, 2005), inundation duration (Friedman and Auble, 1999; Auble *et al*., 2005), erosion rate (Richter and Richter, 2000), sediment deposition depth (Levine and Stromberg, 2001), nutrient flux rate (Antheunisse *et al*., 2006), mechanical stress level (Bendix, 1999) and water-borne propagule delivery rate (Jansson *et al*., 2005b).

In our study, recruitment failure in control areas was due to either the lack of seed or, most commonly, the absence of the requisite patches of bare sediment (Scott *et al*., 1996). The absence of these patches was the consequence of four aspects of the post-dam flow regime: (1) the managed flow regime, including the 1999 flood, failed to produce lateral channel migration sufficient to generate bare soil patches through the process of point bar formation; (2) over the several decades since dam completion high base flows had promoted the establishment of dense herbaceous and shrubby vegetation on all areas with seasonally high water tables, and on the only portions of existing point bars that were also safe from annual scouring; (3) the managed flow regime failed to produce the hydraulic shear stress necessary to scour existing point bar vegetation and (4) the quantity of suspended sediment deposited by the 1999 floodwaters was inadequate to bury the inundated point bar vegetation. Sediment deposition on islands, even where thick, failed to produce habitat for successful establishment because sediment was deposited in dense stands of willow, cattail and other marsh vegetation. In addition, the 1999 flow regime failed to produce a peak stage sufficiently high to wet the extensive higher floodplain surfaces, and the flood had little or no effect on the desert shrubs that have invaded during the past four decades. Using a stage discharge relationship we created during this flood ($y = 0.5875x$, where $y$ is stage in cm, and $x$ is flow in $m^3 s^{-1}$, $R^2 = 0.99$), we estimate that a discharge of 350–425 $m^3 s^{-1}$ is needed to overtop the banks in the study area. Thus, the natural inflow to Flaming Gorge Reservoir during 1999 was suitable for producing an overbank flood (Figure 2 Bottom Panel) if



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outflow had been set to match inflow. Flood discharge magnitude and duration, which largely control inundation, lateral erosion, scour and deposition patterns, including meander rate, are key variables with nonlinear relationships to the rate of creation and areal extent of patches suitable for seedling establishment.

Not all hydrologic alterations shift a riparian community to a novel state that is resistant to flood disturbance. For example, flow management by Derby Dam on the Truckee River in Nevada, which functions as a weir to seasonally divert water for agricultural irrigation, initially resulted in the summer dry-up of the river. This led to adult cottonwood dieback and the curtailment of cottonwood recruitment, similar to what flow regulation produced in our Green River study area. However, Derby Dam provides little water storage capability, captures little sediment and base flows have not been increased. The restoration of flood pulses on the Truckee below Derby Dam has led to successful cottonwood seedling establishment (Rood *et al*., 2003). Unlike flows in the Green River below Flaming Gorge Dam, even managed flows of the Truckee River have been highly variable and, coupled with highly mobile and nearly normal load of sands and gravels, these flows appear to have prevented the system from reaching the threshold initiating transition to a new stable state.

Whether an appropriately designed flood coupled with pre-flood treatments on appropriate landforms can be used to create ecologically significant recruitment depends on the landform treatments, characteristics of the flood, the timing and density of seed delivery, and the rate of attrition among the seedlings established. Seed rain had a clear role in determining initial seedling density in our study (Figure 4). Small-scale spatial variation in cottonwood seed deposition within individual study locations may explain our failure to find a consistent pattern between initial seedling density and treatment type (Figure 5, top panel). Long-term increases in soil carbon could result in increasing C:N ratios, lowering available N for cottonwood seedlings, which may be N-limited (Adair and Binkley, 2002). Interspecific competition with N-fixing plants, such as exotic species of *Melilotus* (sweet clover, Fabaceae), which form thick herbaceous mats in study site bars, could also reduce seedling growth or survivorship (Taylor *et al*., 1999).

The number of saplings in our plots in 2008 was a small fraction of the total number of seedlings that established in our treatment areas following the managed flood. In the most productive area, the P + H treatment at Upper Grimes, seedling density fell from 9.8 to 0.3 individuals $m^{-2}$ between 1999 and 2008. The 2008 density extrapolates to 95 individuals in the full 300-$m^2$ treatment area. However, if the survivorship probability remains constant, these 95 individuals will be reduced to 1 by 2018. This translates to a decline in density to about 2.6 trees $ha^{-1}$ by the time the trees are 15 years old and to 0.25 trees $ha^{-1}$ by age 20, when Fremont cottonwoods in the study area become sexually mature (D.C. Andersen, unpublished data). Cottonwood density in mature stands along the unregulated Yampa River ranges from 39 to 63 trees $ha^{-1}$ (D.C. Andersen, unpublished data). Clearly, not only repeated floods to generate recruitment episodes, but mechanisms to improve survivorship of recruited seedlings and saplings are necessary if existing cottonwoods at Browns Park are to be even partially replaced using recruitment generated through a combination of land treatment and managed flooding.

Ungulates had a deleterious effect on cottonwood saplings in the study area, and other mammalian herbivores are also attracted to young trees (Andersen and Cooper, 2000; Breck *et al*., 2003). Saplings cut by beaver died or are being maintained in a short form that is easily browsed by ungulates, as has occurred among willows in Rocky Mountain National Park, Colorado (Baker *et al*., 2005). Survivorship can be enhanced by using fences to exclude mammalian herbivores (Opperman and Merenlender, 2000; Andersen, 2005), but constructing effective fencing can be difficult and expensive for large areas and for sites subject to flood flows.

Our study suggests that considerable effort can be required to circumvent the resistance of new riparian communities to cottonwood establishment on large rivers with a long history of flow regulation. New approaches are required to manage these riverine ecosystems, as has been suggested for prairies and forests (Seastedt *et al*., 2008). Ongoing, world-wide water resource development will continue to threaten riparian ecosystems (Poff *et al*., 2003). We suggest that management of flows on recently or yet-to-be regulated rivers should strive to maintain or restore native riparian communities downstream of dams early in the dam's existence, and prevent downstream ecosystems from shifting into a new state that is potentially irreversible even with the implementation of relatively large managed floods.

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